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Fungal defense against mycophagy in milk caps

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Abstract Some Basidiomycetes exude latex, but very little is known about the nature of fungal latex. In this study, we examined the nature of latex in *Lactarius* Pers. 1797 spp. to clarify the role on fungivorous predation. In the field, we compared the degree of predation on taxonomically closely related latex-exuding *Lactarius* spp. and latex-non-exuding *Russula* Pers. 1796 spp. (Russulaceae) at developmental stages of sporocarps. We clarified that *Russula* spp. suffered more infestation than did *Lactarius* spp. at young and mature developmental stages, whereas *Lactarius* spp. did only at decaying stages. We measured the amount of latex exuded varied according to developmental stage and sporocarps parts in *Lactarius* spp.: mature sporocarps exuded more latex than did younger ones, while decaying sporocarps exuded the least, and the same patterns were observed at sporocarps parts: the amount of latex was more intense at hymenophore and cap than at stripe. At feeding experiments, three-band garden slugs *Ambigolimax valentianus* Férussac, 1822 avoided feeding on sporophores of *Lactarius* spp. when they exuded latex, but fed on them when they did not. Our observations suggest that fungivores generally escape higher density of the latex at feeding using signs volatized by sporophores with exuding latex.

Key words. *Lactarius*, *Russula*, mycophagy, slug, latex

Introduction

Fruit bodies of several *Lactarius* species (Russulaceae; Russulales), i.e., *Lactarius* volemus, *Lactarius hygrophoroides* Berk. & Curt.1859, *Lactarius corrugis* Peck 1879, *Lactarius akahatsu* Nobuj. Tanaka 1890, *Lactarius hatsudake* Nobuj. Tanaka 1890, and *Lactarius laeticolorus*, (S. Imai) Imazeki ex Hongo 1960 are appreciated in Japan, where they are considered to be delicious mushrooms. There are also pungent tasting species; however, a characteristic common to all species in the genus is that they exude milk or latex when the sporocarps are damaged. The milk exudes from lactiferous hyphae distributed under the surface of the entire fruit body. The main content of the milk in *L. volemus* has been identified as polyisoprene, which is the same compound found in the rubber that exudes from the rubber tree, *Hevea brasiliensis* (Ohya et al. 1998).

Several species of rubber trees (Euphorbiaceae: Euphorbiales) that have been planted to produce rubber are well-known to yield latex from bruised leaves, although the physiological function and ecological significance of this phenomenon has been subject to scant study (Light and Dennis 1989). This phenomenon is not ex-

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clusive to rubber trees; in angiosperms, 10 % of plant species ($> 20,000$ species among 40 families in multiple lineages) exude latex upon tissue damage; this latex has no known function in the primary metabolism (Farrell et al. 1991; Hunter 1994; Lewinsohn 1991). Historically, several types of evidence have implied that the latex acts as a potent plant defense against herbivores (Fellows et al. 1986; Hartmann 1991). In the past two decades, increasing numbers of studies have emerged on latex, its biochemistry, and its ecological and evolutionary consequences, with special reference made to plant-herbivore interactions (e.g., Konno et al. 2004; Konno et al. 2006; Agrawal and Konno 2009). To date, no study has explored the ecological role of latex in fungal sporocarps during fungi-fungivory interactions. We adapt the comparative ecological approach to clarify the role of latex in *Lactarius* spp. on the interaction between the sporocarps of the genus *Lactarius* and *Russula*, mainly due to that 1) the sporocarps of *Lacrarius* exudes latex, whereas those of *Russula* do not, and 2) these two genera are taxonomically closely related in family Russulaceae (Miller et al. 2006), and 3) their habitats are often largely overlapped in a field. Additionally, many characteristic feeding marks by slugs were often observed on the *Russula* sporocarps in a field. However, no study clarifies the feeding behaviours of slugs on fungi except for Worthen (1988).

In this study, we examined the animal community, mainly focused on arthropods and slugs, on *Lactarius* spp. and sympatric *Russula* spp. in relation to the developmental stages (i.e., young, mature, and decaying stage) of sporocarp in a field. Furthermore we investigated the amount of latex in relation to the developmental stages and the sporocarp parts (i.e., cap surface, hymenophore, and stipe). Additionally, we performed feeding experiments using slugs to confirm the role of latex on the fungivorous predation.

Materials and Methods

Field sampling

We collected species of *Lactarius* and *Russula* sporocarps in various broad-leaf and coniferous forests ($136°33' - 137°45'$E, $36°25' - 37°18'$N, altitude ca. $50 - 1000$m) located in Ishikawa and Toyama prefectures of western Japan, from July to November in 2013. The collected sporocarps were brought back to the laboratory, in a cool box to avoid desiccation, for further analysis. We recorded fungal species (Ikeda 2005, 2013), developmental stage (young: cap is undeveloped; mature: cap is developed; decaying: flesh has started to deteriorate), and the presence of any trace of predation in the respective sporocarps. We also recorded for feeding marks on the sporocarps in the field. The round-shaped feeding marks can be identified by characteristic signs of scraping by slugs. We collected insects that had gathered around sporocarps using an aspirator, with the aid of a hand net, and kept them in ethanol for identification at the genus or species level (Ueno et al. 1985; Okada and Suzuki 1988; Disney et al. 2014) under a microscope in the laboratory. Insect specimens that we were unable to identify were sent to specialists for identification (specialists are named in the Acknowledgements section). To check for the presence of breeding insects within sporocarps, fungal samples were weighed and placed on moist vermiculite, in containers of an appropriate size, at $23 \pm 1°$C under 14-h light/10-h dark photoperiod conditions. Each container lid had a hole plugged with cotton wool to ensure adequate air exchange. The sporophores were misted with water to maintain sufficiently high humidity. The containers were checked for emerging insects every 1 or 2 days, for at least 1 month after sporophore collection. The collected emerged insects were identified as described above.

Quantification of latex in sporocarps of Lactarius spp.

We quantified the amounts of latex exuded from three parts of the collected *Lactarius* sporocarps: the cap, hymenophore, and stipe. On each part, we cut a slash (1-cm length, 0.5-cm depth, 0.1-mm width) in a flawless section using a blade (FA-10, Feather Safety Razor Co., Ltd. Osaka, Japan) to quantify the exuded latex using a microcapillary tube (Accu-Fill 90 Mi-cropet, Clay Adams Co., Ltd., New York, NJ, USA). The angles of the slashes were vertical from top to the bottom (hymenophore) in the cap, vertical and across at right angles to lamella in the hymenophore, and horizontal in the stipe (Figure 1). Slashes were made three times and exuded latex was averaged in each part. We measured exuded latex in the young, mature, and decaying stages of sporophores.

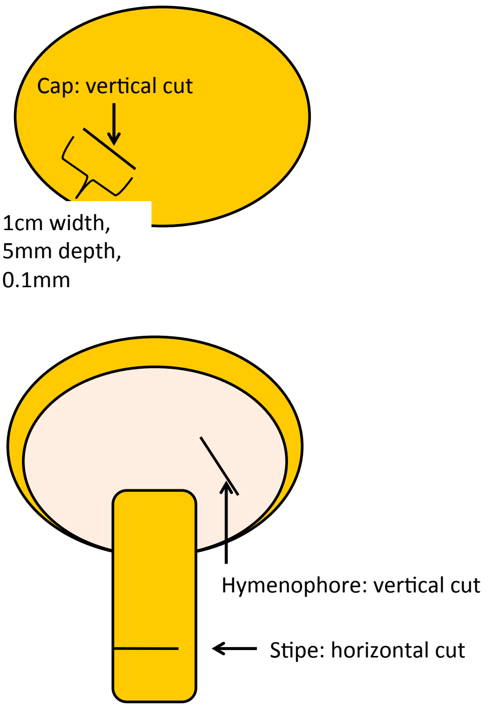

Figure 1. Cut angle in *Lactarius* sporocarps for measuring the volume of latex exuded.

Feeding experiments by slugs

To observe their feeding behaviour, we collected wild three-band garden slugs *Ambigolimax valentianus* Férussac, 1822 (Limacidae, Stylommatophora, Gastropoda, Mollusca), in October 2013 from the Kanazawa University campus. We observed their feeding behaviour via the following two groups of experiments in a laboratory:

Group A: Mature sporocarps of *Lactarius akahatsu, L. hatsudake, L. chrysorrheus* Fr. 1838 and *Russula pseudointegra* Arnould & Goris 1907 were collected in October 2013. Two sporocarps of one of the three *Lactarius* species and two of *R. pseudointegra* were placed individually in plastic petri dishes (four dishes in total, each 9 cm in diameter), which were then laid equidistantly in a plastic case (35 × 25 × 19.5 cm in height) with a plastic mesh ridge to allow air exchange. Five slugs were introduced and allowed to feed on the sporocarps, and wet tissue was laid in the bottom of the case to facilitate the slugs movement. This set-up was replicated for each of the three *Lactarius* species, so that six *Lactarius* and six *R. pseudointegra* were tested with 15 slugs simultaneously. The cases were placed in an incubator (22°C, 14 hours light/10 hours dark), and the slugs'feeding was checked and recorded every 8 hours, for a total of nine times over the first 72 hours after introduction.

Group B: The basic set-up was the same as for Group A, with each of the three *Lactarius* species plus *R. pseudointegra*. However, we made a 2-cm-wide by 0.5-cm-deep incision into the cap, hymenophore, and stipe of all *Lactarius* sporocarps using a sharp blade to allow latex to ooze out.

Results

Arthropod community on Lactarius spp. and Russula spp.

We collected 300 sporocarps from 30 species in the Russulaceae. Of these, we collected 874 arthropods from 24 of 78 *Russula* sporocarps and 45 of 222 *Lactarius* sporocarps. Mobile arthropods collected at various stages of sporocarp maturity and senescence are shown in Table 1. In young sporocarps, we found no arthropod from *Lactarius* spp. and only five from *Russula* spp. (Table 1). In mature sporocarps, we again found no arthropods from *Lactarius*, but collected 279 from *Russula* (Table 1). The dominant groups included four species of

Table 1. Taxonomic groups of arthropods collected from young, mature, and decaying *Lactarius* (L) and *Russula* (R) sporocarps in the field

	young		mature		decaying	
Order Family Species	L	R	L	R	L	R
Blattodea						1
Coleoptera						
Leiodidae						
Cyrtusa japonica Champion, 1925					22	
Pseudocolenis strigosulus (Portevin 1905)					1	
Staphylinidae						
Acidota crenata (Fabricius 1792)					1	
Atheta weisei Bernhauer 1907					3	
Gyrophaena nipponensis Cameron 1933					171	
Oxyporus sp.				1		
Priochirus japonicus Sharp 1889					1	
Diptera						
Cecidomyiidae						1
Chironomidae				1		
Chloropidae					1	1
Clusiidae				1		
Drosophilidae						
Drosophila angularis Okada 1956				12	2	27
Drosophila bizonata Kikkawa & Peng 193				15	3	9
Drosophila brachynephros Okada 1956				11	1	15
Hirtodrosophila sexvittata Okada 1956				1	3	6
Muscidae						
Muscina angustifrons (Loew 1858)		1		5		
Mycetophilidae						
Exechia arisaemae Sasakawa 1993		1				
Otitidae						1
Phoridae						
Megaselia flava (Fallen 1823)				2		3
M. gotoi Disney 1989		3		1		
M. kanekoi Disney 1989				2		2
M. donaldsonae Disney et al. 2014				3	2	2
Megaselia sp.				1		1
Sciaridae						1
Sphaeroceridae						4
Hymenoptera						
Formicidae					3	
Parasitoidic wasp				3		
Collembora						
Hypogastruridae						
Ceratophysella cf. horrida				31	23	31
Ceratophysella denisana (Yosii 1956)				67	71	
Ceratophysella denticulta (Bagnall 1941)				101	153	22
Ceratophysella pilosa (Yosii 1956)				21		
Pseudoscorpionida					2	
Total number of individual	0	5	0	279	463	127
Number of sporocarps	41	23	60	25	21	30
Density per sporocarp	0	0.2	0	11.2	22.0	4.2

Table 2. Composition of insects emerged from *Lactarius* (L) and *Russula* (R) sporocarps

Order Family Species	young L	young R	mature L	mature R	decaying L	decaying R
Diptera						
Chloropidae						2
Drosophilidae						
Drosophila angularis			1		2	1
D. bizonata					40	
D. brachynephros					6	
D. unispina Okada 1956					2	
Hirtodrosophila alboralis (Momma & Takada 1954)					1	
H. histrioides Okada & Kurokawa 1957			17		296	3
H. sexvittata					4	1
Mycodrosophila gratiosa			10		27	
M. poecilogastra (Loew 1874)					23	
Lonchaeidae					14	1
Muscidae						
Muscina angustifrons			104	229	30	38
Mycetophilidae					1	1
Phoridae						
Megaselia sp.			1	1		
M. donaldsonae					2	
M. flava					2	5
Psychodidae					5	
Sphaeroceridae					2	
Tiplidae					7	
Hymenoptera						
not identified (Parasitoidic wasp)					2	
Total number of individual	0	0	133	230	466	52
Number of sporocarps	41	23	60	25	21	30
Density per sporocarp	0	0	2.2	9.2	22.2	1.7

collembola (78.9% of the 279-individual total), four species of drosophilid (14.0%), five species of phorid (3.2 %), and *Muscina angustifrons* (Loew, 1858) (1.8%) (Table 1). In decaying sporocarps, we found 463 arthropods from *Lactarius*, dominated by collembola (53.3 %) and beetle species (leodids and staphylinids, 43.0 %), while 127 were collected from *Russula*, dominated by drosophilids (44.9 %), collembola (41.7 %), and phorids (6.3 %) (Table1). Larval species composition is represented as emerged adults, and summarised in Table 2. Mycophagous dipteran larvae normally grow within the sporocarp until emergence. Therefore, insect fauna of sporocarp is characterised by lower mobility. No adult emerged from young sporocarps of either genus (Table 2). In mature *Lactarius, M. angustifrons* was most abundant (78.2 % of 133 individuals) followed by *Hirtodrosophila histrioides* Okada & Kurokawa 1957 (12.8 %) and *Mycodrosophila gratiosa* (Meijere 1911) (7.5 %), while *M. angustifrons* dominated in *Russula* (99.6 % of 230 individuals). Diverse dipteran insects (eight families, nine drosophilid species, and three Megaselia spp.) emerged from decaying *Lactarius*, of which drosophilids (86.1 % of 466 individuals) and *M. angustifrons* (6.4 %) were most abundant, while in *Russula*, less diverse diptera (six families, four drosophilid species, and one *Megaselia* sp.) emerged and were dominated by *M. angustifrons* (73.1 % of 52 individuals). Sporocarps of the two genera with all types of feeding marks and with only slug-derived marks are summarised in Table 3. We found no feeding marks in young sporocarps

Table 3. Percentage (%) of *Lactarius* (L) and *Russula* (R) sporocarps with animal feeding marks (all kinds of animal or slugs alone) in the young, mature, and decaying stages.

developing stage	young			mature			decaying		
	L	R	*P*	L	R	*P*	L	R	*P*
Number of sporocarp	14	6		200	44		73	56	
All kind of feeding mark	22%	50%	NS	9%	50%	<0.01	32%	68%	<0.01
Feeding marks of slug	0%	0%	NS	3%	21%	<0.01	18%	43%	<0.01

Table 4. Amount of latex exuding from caps, hymenophores, and stipes in the *Lactarius* species sampled

species	Number of sporocarp	Mean±SE (μl)		
		Cap	Hymenophore	Stipe
Lactarius akahatsu Nobuj. Tanaka 1890	6	0.10±0.00	0.10±0.00	0.10±0.00
L. chrysorrheus Fr. 1838	7	6.86±2.38	16.86±4.70	3.79±1.75
L. lividatus Berk. & M.A. Curtis 1860	3	0.10±0.00	0.10±0.00	0.100±0.00
L. subvellereus Peck 1898	1	1	1	2
L. piperatus (L.) Pers. 1797	3	2.33±0.88	4.67±0.67	1.00±0.58
L. quietus (Fr.) Fr. 1838	28	1.81±0.56	5.53±1.37	1.19±0.47
L. subpiperatus Hongo 1964	12	3.28±1.55	3.87±1.55	1.45±0.60
L. volemus (Fr.) Fr. 1838	118	10.16±1.31	18.39±1.99	7.59±1.32
Lactarius sp.1	1	5	17	0
Lactarius sp.2	2	0	0.05	0

of either genus (Table 3). In mature and decaying sporocarps, we found fewer feeding marks in *Lactarius* for all animals and for slugs alone (Fishers exact test for no. of sporocarps with marks, $P < 0.01$, Table 3).

Quantification of latex

We quantified the exuded latex of 181 sporocarps from 10 species (Table 4). In general, hymenophores exuded the most latex among the three parts incised (Table 4). We statistically compared the volume of latex in reference to the sporocarp only for the two most abundant species, *L. volemus* and *L. quietus*. Latex volumes varied among sporocarps depending on environment, and we expressed the volumes as proportions of the volume of latex from the stipe to that from the respective sporocarp (Fig. 2A). We found a significant difference in latex volume among parts of mature sporocarps, wherein hymenophores exuded the most, followed by caps, and finally stipes ($N = 64$, Kurskal-Wallis nonparametric test with Steel-Dwass test, $P < 0.05$, Fig. 2A) in *L. volemus*. Hymenophores exuded more latex than stipes in mature *L. quietus* ($N = 13$, $P < 0.05$, Fig. 2A). In *L. volemus*, more latex was exuded from hymenophores in mature and young stages than in the decaying stage ($N = 119$, $P < 0.05$, Fig. 2B).

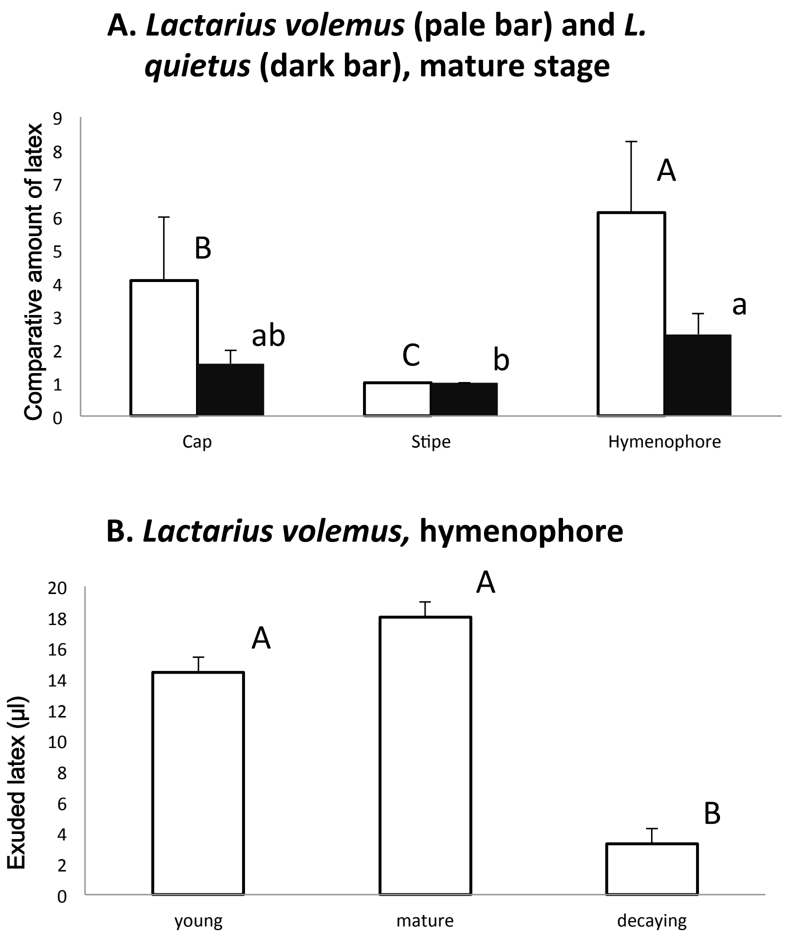

Figure 2. Comparative latex volume in different parts of mature *Lactarius volemus* and *L. quietus* (Fr.) Fr. 1838 (2A) and different developmental stages in *L. volemus* hymenophores (2B). Different letters indicate statistical significance ($P < 0.05$) in respective species between different parts or different developmental stages.

Feeding experiments by slugs

Group A: All *Lactarius* species exuded latex within 16 hours of feeding by slugs and were not fed on again for at least 48 hours. One *L. hatsudake* that stopped exuding after 64 hours was later fed on by one slug in the stipe (at 64 hours) and a further two slugs in the stipe and hymenophore (at 72 hours). Five sporocarps – the other *L. hatsudake*, two *L. akahatsu*, and two *L. chrysorrheus* – were not fed on after the first feeding and were still exuding at the end of observations, 72 hours later. Contrary, all six *R. pseudointegra* were fed on by at least one of five slugs (two slugs in one case) over the three days. Feeding marks were observed on every part of the sporocarp: hymenophore, cap, and stipe. All R. *pseudointegra* appeared to be in the mature stage without desiccating or decaying by the end of observation.

Group B: All sporocarps were incised to make the *Lactarius* exude before exposure to slugs. All but two *Lactarius* were free from feeding marks for 72 hours, and were still exuding 72 hours later. One *L. akahatsu* was fed on, and one *L. chrysorrheus* had gained marks in the stipe at 64 hours and in the hymenophore at 72 hours. Due to desiccation, neither was exuding latex at the end of observations. All six *R. pseudointegra* had feeding marks on their hymenophores, caps, and stipes. All *R. pseudointegra* appeared to be in the mature stage without desiccation or decay by the end of the observation period.

Discussion

We found less infestation in *Lactarius* sporocarps than in sympatric *Russula*, another member of the Russulaceae. In field observations, we found few arthropods visiting mature *Lactarius* sporocarps. The lack of arthropods visiting or

emerging from the young stages of both *Lactarius* and *Russula* may be due to the relatively short exposure time, or some type of repellent effect. While few or no arthropods visited or emerged from mature *Lactarius*, many collembola and flies visited mature *Russula*. By contrast, we found more collembola and beetles on, and more diverse flies emerging from, decaying *Lactarius*. These differences could be due to physical features: most decaying *Lactarius* sporocarps were dry, whereas most decaying *Russula* ones were sludgy inside and misshapen. Because collembola and beetles feed mainly on surfaces, the most abundant group on decaying *Lactarius* sporocarps was beetles, whose mandibles enable them to scrape the desiccated surfaces of the sporocarps. The most abundant among larvae were a diverse group comprising *Hirtodrosophila* and *Mycodrosophila* spp. These two genera are known to feed and breed more on the comparatively hard sporocarps of the Pleurotaceae and Polyporaceae than other mycophagous drosophilids (Tuno 1998, 1999, 2001; Toda et al. 1999; Takahashi et al. 2005). Interestingly, the most common species in mature and decaying *Russula* was *Muscina angustifrons* (Muscidae, Diptera), an opportunistic predatory species that feeds on dipteran larvae within the same sporocarp (Akaishi and Nakamura 2015). Perhaps this predator prefers laying eggs on *Russula* over *Lactarius*, and this difference may contribute to the diverse and abundant dipteran flies emerging from decaying *Lactarius* sporocarps.

In this study, the ratio of wild sporocarps with feeding marks was also significantly lower in mature and decaying stages of *Lactarius* but was not significant in the immature stage with respect to feeding marks caused by all animals, or by slugs alone. Latex oozing was generally higher in the young and mature stages than in the decaying stage for all species, and in hymenophores and caps than in stipes. Our predation avoidance by latex hypothesis predicts that latex abundance may vary among mature stages and fruit body parts in a manner consistent with relative contribution to fitness. For example, fruit bodies of *Amanita muscaria* (L.) Lam. (1783) contain ibotenic acid which is lethal to flies. The highest concentration of ibotenic acid was detected in the caps that produce spores in the immature stages (Tsunoda et al. 1993). Similar result of amanitin has been reported in lethal mushroom, *Amanita exitialis* Yang and Li 2001 (Hu et al. 2012). These observations suggest that lethal toxins are produced selectively and distributed specifically in the immature stages and in the caps as a defense against predation. That more latex oozing was observed in the young and mature stages, and in hymenophores and caps, is consistent with the predation avoidance hypothesis.

In feeding experiments, it was clear that slugs, *Ambigolimax valentianus*, avoided feeding on *Lactarius* sporocarps when they exuded latex. Thus, milk caps apparently receive slug predation only when they are intact or degraded but not exuding latex. To this end, we have rarely come across flies around *Lactarius* species in the field, though we have seen many gathered around sympatric *Russula* sporocarps. Therefore, we assume that *Lactarius* spp. release volatiles that repel a wide range of arthropods and slugs when they are exuding. Various mushroom-characteristic volatiles, such as 1-octen-3-ol and lenthionine, are known to science (Maga 1981). It has been reported that 1-octen-3-ol is increasingly released upon tissue damage to sporocarps, and repels slugs and collembola (Sawahata et al. 2008; Wood et al. 2001). Though volatiles have been reported in some *Lactarius* species (Pyysalo 1976), we have not detected their characteristic strong odour in the field or in the laboratory. Poly-isoprene, the main constituent of *L. volmes* emulsion, initiates a condensation reaction when in contact with air, releasing volatiles such as lactone (Morand 1977). As this condensation reaction progresses polyisoprene indurates, and the sporocarp hardens. Therefore, old and hard sporocarps will not release volatiles of sub-products of the condensation reaction. Further biochemical studies are needed to test our hypothesis: we must identify volatile variation relating to sporocarp development and bioassay them to determine their ecological functions against diverse mycophagous animals.

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